

Triassic coniform conodont genera *Aduncodina* and *Neostrachanognathus*

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Abstract. Lower Triassic coniform conodonts *Aduncodina unicosta* Ding and *Neostrachanognathus tahoensis* gen. et sp. nov. from the pelagic limestone of the Taho Formation in Ehime Prefecture, Southwest Japan are newly reconstructed as quadrimembrate apparatuses with the M, Sa, Sb, and Sc elements. *A. unicosta* Ding, originally described as a form species, is the Sb element of the skeletal apparatus of *A. unicosta*, newly conceived. Furthermore, the form species *Cornudina anterodentata* Ding and *C. angularis* Wang and Cao are referable to the Sa and Sc elements of *A. unicosta*, respectively. The elements of *A. unicosta* and *N. tahoensis* are all coniform types. The M elements of the two species are adenticulated and the Sa, Sb, and Sc elements are denticulated with one to four denticles on the anterobasal margin of the base. The morphologic similarity between Triassic *A. unicosta* and *N. tahoensis* and the Early to Middle Paleozoic coniform-type conodonts probably represents an adaptive convergence of the feeding apparatuses. *A. unicosta* and *N. tahoensis* indicate the early Spathian.

Key words: *Aduncodina unicosta* Ding, coniform conodonts, *Neostrachanognathus tahoensis* gen. et sp. nov., quadrimembrate apparatus, Taho Formation, Triassic.

Introduction

A form species of conodont, *Aduncodina unicosta* Ding, was recovered by Ding (1983) from the Lower Triassic Helongshan Formation of Mt. Majiashan of Chaoxian, Anhui Province, South China. This species is a coniform element characterized by a nongeniculate, slender, and suberect cusp and the presence of one to three hook-like denticles on the anterobasal margin of the base.

This uniquely shaped conodont also occurs abundantly in the pelagic limestone of the Triassic Taho Formation exposed at Tahokamigumi, Shirokawa-cho, Higashi-uwagun, Ehime Prefecture, Southwest Japan (Figure 1). As a result of statistical analysis of the conodont fauna, including the form species *A. unicosta*, it has been made clear that this form species is one of the elements of a quadrimembrate skeletal apparatus composed of the M, Sa, Sb, and Sc elements. The M element is an adenticulated and the Sa, Sb, and Sc elements are denticulated nongeniculate coniform types with one to four denticles on the anterobasal margin of the base. The form species *A. unicosta* of Ding (1983) is the Sb element of the apparatus. Furthermore, the form species *Cornudina anterodentata* Ding and *C. cf. oezdemirae* Gedik described by Ding (1983) from the same sample yielding *A. unicosta* can be regarded as the Sa and Sc elements of the apparatus, respectively. The form species *C. angularis* Wang and Cao (1993) from the Upper

Chinglung Formation of the Early Triassic at Jiangning in Nanjing can be also referred to the Sc element of the skeletal apparatus.

I propose herein *Aduncodina unicosta* Ding for this quadrimembrate skeletal apparatus composed of four coniform type elements. *Aduncodina unicosta* is an index of the early Spathian.

In the Taho Formation there occurs another quadrimembrate coniform species. The elements are basically common in morphology with those of *A. unicosta*. The M element is an adenticulated and the Sa, Sb, and Sc elements are denticulated nongeniculate coniform types with one denticle on the anterobasal margin of the base.

I also propose herein *Neostrachanognathus tahoensis* gen. et sp. nov. for the quadrimembrate conodont species. *Cratognathodus* sp. reported by Buryi (1989) from the Spathian in the Dalnegorsk region, Sikhote-Alin is the Sb element of this new species. *Neostrachanognathus tahoensis* indicates the early Spathian.

Coniform elements are considerably dominant components in apparatuses of conodonts diversified during the Late Cambrian to Devonian but quite rare or almost absent in the post-Devonian Paleozoic. The reconstruction of coniform conodont apparatuses is, therefore, very important for the study of evolution of the Conodonts. I describe the skeletal apparatuses of *A. unicosta* and *N. tahoensis* and consider the phylogeny of these genera comparing with



Figure 1. Index map showing the location of the study section. 1a. Index map. Th: Tahokamigumi. 1b. Solid circle shows the outcrop section of Tahoe Formation at Tahokamigumi, Shirokawa-cho, Higashiuwa-gun, Ehime Prefecture, Southwest Japan.

Cornudina in the Triassic and some coniform apparatuses in the Paleozoic.

All of the described specimens are kept in the Department of Science Education, Faculty of Education and Human Sciences, Yokohama National University.

Biostratigraphic setting

Aduncodina unicastra and *N. tahoensis* are restricted respectively within the basal 2 and 4 m of the Spathian *Neospathodus triangularis*-*N. homeri* Zone (8 m thick) in the Triassic Tahoe Formation (Figure 2). The Spathian limestone is composed of dark gray, thin- to medium-bedded biomicrite including abundant thin-shelled bivalves and radiolarians and subordinate echinoderm crusts, small gastropods, and foraminifers. This lithologic feature indicates that the limestone is pelagic in origin. An estimated sedimentation rate is about 0.5-0.8 g/cm²/1,000 yr (Koike, 1994).

In the Tahoe Formation, *A. unicastra* and *N. tahoensis* occur

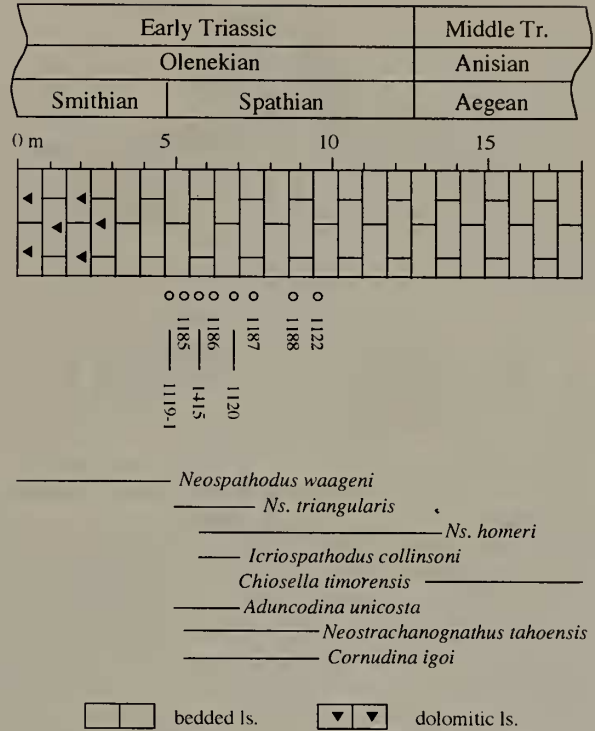


Figure 2. Stratigraphic section and vertical distribution of *Aduncodina unicastra* Ding, *Neostrachanognathus tahoensis* gen. et sp. nov., and important pectiniform conodonts.

with *Neospathodus triangularis* (Bender), *N. homeri* (Bender), *Icriospathodus collinsoni* (Solien), *Cornudina igoi* Koike, *El-lisonia triassica* Müller, *E. dinodoides* (Tatge), and many unidentified coniform and ramiform elements. Among them, the first four species are restricted to the Spathian.

The form species *A. unicastra* proposed by Ding (1983) for the Sb element of the *A. unicastra* apparatus is associated with *N. triangularis*, *N. homeri*, and *I. collinsoni* in the Helongshan Formation in Anhui Province, South China. The form species *Cornudina angularis* proposed by Wang and Cao (1993) for the Sc element of the *A. unicastra* apparatus occurs in the Upper Chinglung Formation in Nanjing which yields *N. triangularis* and *N. homeri*. Consequently, the occurrence of the *A. unicastra* apparatus in South China well accords with that of Japan in age.

Cratognathodus sp., described by Buryi (1989) from the Spathian of Sikhote-Alin can be assigned to the Sb element of the *N. tahoensis* apparatus. The biostratigraphic range of *N. tahoensis* also accords with that established in Japan.

The apparatus of *Aduncodina unicastra* Ding

Aduncodina unicastra is reconstructed as a quadrimembrate skeletal apparatus in this study (Figure 3). The elements are composed of an adenticulated, a denticulated bilaterally subsymmetric, and two denticulated asymmetric nongeniculate coniform types. The denticulated coniform elements carry one to four anterobasal denticles. I assign

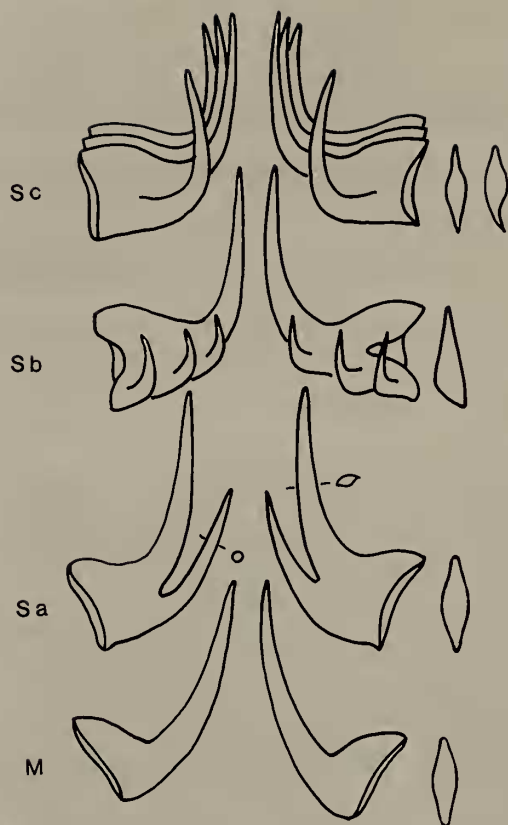


Figure 3. A hypothetically reconstructed apparatus of *Aduncodina unicosta* Ding. All elements are arranged in symmetric pairs.

the adenticulated subsymmetric coniform element to the M, the denticulated subsymmetric one to the Sa, and the asymmetric denticulated ones to the Sb and Sc positions, respectively.

The frequency of the M, Sa, Sb, and Sc elements in four samples is 20, 84, 58, and 181 and an approximate ratio of the elements is 0.3:1.5:1:3.1, respectively (Table 1). Triassic *Ellisonia dinodoides* (Tatge) statistically reconstructed by Koike (1994) comprises the M (breviform digyrate), Sa (bilaterally symmetric alate), Sb (extensiform digyrate), Sc (bipennate) elements whose inferred ratio is 2:1:2:4 or 6. Paleozoic ozarkodinid apparatuses reconstructed based on natural assemblages are composed of the M (breviform digyrate), Sa (alate), Sb₁ (bipennate), Sb₂ (bipennate), Sc₁ (bipennate), Sc₂ (bipennate), Pa (carminiscaphate), and Pb (angulate) elements, the ratio among which is 2:1:2:2:2:2:2:2 (Purnell and Donoghue, 1998, etc.). The composition of the apparatus of the Pennsylvanian prioniodinid *Gondolella* is almost the same as for the ozarkodinids (von Bitter and Merrill, 1998). *Aduncodina unicosta* has, therefore, relatively rare M elements and abundant Sa elements compared with those previously confirmed multielement apparatuses with ramiform (M and S series) and pectiniform (P series) elements.

According to Dzik and Drygant (1986), the Sa (tr) element

Table 1. Occurrence of M, Sa, Sb, and Sc elements of *Aduncodina unicosta* Ding obtained from 5 to 10 kg of limestone.

Loc.	M	Sa	Sb	Sc
1119-1	2	3	4	19
1185	1	9	2	15
1415	16	63	45	111
1186	1	9	7	36
total	20	84	58	181
ratio	0.3	: 1.5	: 1	: 3.1

is bilaterally subsymmetric and considered to be paired in most coniform apparatuses in the Ordovician. The relative abundance of the Sa element in the *A. unicosta* apparatus may be comparable to the above-mentioned feature of the Ordovician coniform apparatuses.

It is, however, difficult to explain why the occurrence of the M element is rare compared with that of the Sa and Sb elements in the *A. unicosta* apparatus. Further study is necessary to confirm the positions and proportions of the elements in *A. unicosta* based on more abundant specimens.

The four elements considered to be of the *A. unicosta* apparatus have common morphologic characteristics such as thin wall, suberect cusp, moderately deep basal cavity, and hook-like anterobasal denticles in the S series. The morphologic characteristics of each element are as follows.

The M element is a bilaterally subsymmetric adenticulated coniform type.

The Sa element is a bilaterally subsymmetric coniform type with one proclined denticle on the anterobasal margin.

The Sb element is a bilaterally asymmetric coniform type with the triangular basal margin and one to three laterally curved hook-like anterobasal denticles.

The Sc element is a bilaterally asymmetric coniform type with the lenticular basal margin and one to four laterally curved hook-like anterobasal denticles.

The apparatus of *Neostrachanognathus tahoensis* gen. et sp. nov.

The skeletal apparatus of *N. tahoensis* is quadrimembrate and consists of an adenticulated, a denticulated subsymmetric, and two denticulated asymmetric nongeniculate coniform elements (Figure 4). The denticulated asymmetric elements bear one or two anterobasal denticles. I regard the subsymmetric adenticulated element as the M, the subsymmetric denticulated one as in the Sa, and the asymmetric denticulated ones as in the Sb and Sc positions, respectively.

The total number of the M, Sa, Sb, and Sc elements from six samples is 18, 39, 41, and 85 and an approximate ratio of the elements is 0.4:1:1:2, respectively (Table 2). The relative small number of the M and large number of the Sa elements in this skeletal apparatus show the same tendency with the *A. unicosta* apparatus.

The four elements possess common characteristics such as thick wall, suberect to proclined and tapering cusp,

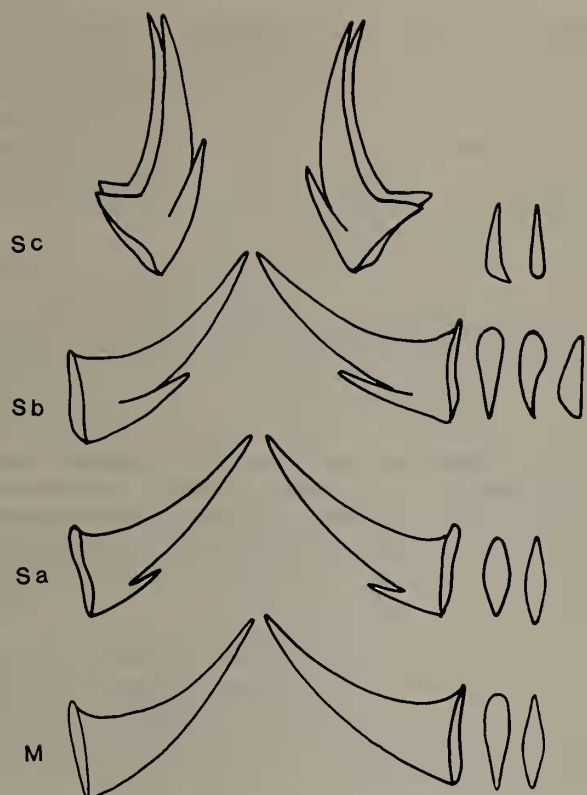


Figure 4. A hypothetically reconstructed apparatus of *Neostrachanognathus tahoensis* gen. et sp. nov. All elements are arranged in symmetric pairs.

Table 2. Occurrence of M, Sa, Sb, and Sc elements of *Neostrachanognathus tahoensis* gen. et sp. nov. obtained from 3 to 5 kg of limestone.

Loc.	M	Sa	Sb	Sc
1185	1	3	4	8
1415	3	6	7	8
1120	9	29	28	67
1186	3	1	1	1
1188	1	0	1	0
1122	1	0	0	1
total	18	39	41	85
ratio	0.4	: 1	: 1	: 2

shallow basal cavity, and one or two small to large antero-basal denticles in the S series. The morphologic characteristics of each element are as follows.

The M element is a bilaterally subsymmetric adenticulated coniform type.

The Sa element is a bilaterally subsymmetric coniform type with one denticle on the anterobasal margin.

The Sb element is a bilaterally asymmetric coniform type with one or two anterobasal denticles bending inwardly.

The Sc element is a bilaterally asymmetric coniform type with the posteriorly extending base and one or two antero-basal denticles bending inwardly. A small denticle may be present on the posterior portion of the base.

Coniform conodonts in the Triassic

As mentioned above, coniform elements are dominant components in the apparatuses of most conodont genera and species in the Late Cambrian to Devonian but are quite rare or almost absent in the Carboniferous and Permian. In the Triassic, coniform conodont elements are also rare but more common than in the Carboniferous and Permian.

In addition to *A. unicosta*, *Zieglericonus rhaeticus* Kozur and Mock was previously proposed as a coniform type and some coniform conodonts were assigned to *Cornudina* or allocated as an unidentified genus.

Zieglericonus rhaeticus proposed by Kozur and Mock (1991) for the coniform element occurred in the upper Rhaetian of Hungary. This species is characterized by a proclined to erect cusp with fine striations and a deeply excavated basal cavity.

Genus A reported by Hatleberg and Clark (1984) from the upper Spathian of Nepal consists of three nongeniculate coniform elements of the alate (Sa), digyrate (M or Sb), and bipennate (Sc) types. They did not describe whether the three elements are of one or more apparatuses. It is probable that the alate type (Pl. 4, fig. 14 of Hatleberg and Clark, 1984) is of a multielement species, the digyrate (Pl. 4, fig. 15) and bipennate (Pl. 4, figs. 11, 12) types are of another multielement species judging from the same type elements occurring in the Spathian of the Taho Formation.

The form genus *Cornudina* was recently reconstructed as a unimembrate or bimembrate apparatus on the basis of samples from the Taho Formation and two species were proposed for the *Cornudina* apparatuses by Koike (1996).

The bimembrate *Cornudina* apparatus, *C. breviamulis* (Tatge) is the type species of *Cornudina* and consists of the segminate pectiniform Pa and angulate pectiniform Pb elements. The Pa element is composed of a long cusp and short anteroposterior processes with one to four denticles. The Pb element consists of a large cusp, a short anterior process with one to five denticles, and a relatively long twisted posterior process with four to seven denticles (Figure 5).



Figure 5. A reconstructed apparatus of *Cornudina breviamulis* (Tatge).



Figure 6. A reconstructed apparatus of *Cornudina igoi* Koike.

The pectiniform Pa and Pb elements of *C. breviramulis* reveal evolutionary trends of decrease in size of the processes and in number of denticles on the processes during Early to Late Triassic times and some of the Pa elements in the Middle and Late Triassic appear to be coniform.

The unimembrate *Cornudina* apparatus, *C. igoi* enacted by Koike (1996), is composed of the segminate pectiniform Pa elements with a long cusp and a very short anterior process carrying one to three denticles (Figure 6). *Cornudina igoi* is restricted within the early Spathian. The elements of *C. igoi* with one anterior denticle look like a coniform type and fairly resemble the Sa element of *N. tahoensis*.

Cornudina was allocated to the genus *Chirodella* of the family Xaniognathidae by Sweet (1981). Koike (1996) separated *Cornudina* from *Chirodella* because the elements of their apparatuses are completely different. It is very difficult to determine the phylogenic position of *C. breviramulis* and *C. igoi* in the family-group category because both species are different in combination and morphology of apparatus elements from the previously proposed conodont groups in the Triassic. I regard *Cornudina*, however, as belonging to the family Gondolellidae because the segminate Pa elements of *C. breviramulis* and *C. igoi* and the angulate Pb elements of *C. breviramulis* indicate some morphologic similarities with the Pa and Pb elements of the family Gondolellidae proposed by Sweet (1988), respectively.

Early Anisian *Cornudina oezdemirae* proposed by Geidik (1975) and late Anisian *C. unidentata* proposed by Kozur and Mostler (1972) are coniform types whose generic names should be reexamined.

The Tahoe Formation yields more than eight types of coniform elements besides those in *A. unicosta* and *N. tahoensis*. I have not reconstructed yet any apparatuses based on the elements because they are not abundant in number. They are, however, referable to 3 or 4 multielement species judging from their occurrence in the strata. More than five coniform multielement species are, therefore, present in the Tahoe Formation.

Phylogeny of *Aduncodina* and *Neostrachanognathus*

Most Early Triassic conodonts previously described belong to the family Sweetgnathidae and Spathognathodontidae of the order Ozarkodinida, the family Ellisoniidae and Gondolellidae of the order Prioniodinida (Sweet, 1988). The apparatuses of these families in the late Paleozoic are composed of six to eight types of elements with the pectiniform P

elements in the P position and ramiform elements in the M and S positions but some lineages lost elements in the Triassic, becoming quinquimembrate with ramiform elements in the M and S positions or unimembrate with a pectiniform element in the Pa position (Sweet, 1988, etc.). Skeletal apparatuses with coniform elements are uncommon in the Ozarkodinida and Prioniodinida which ranged from the Early or Middle Ordovician through the Triassic.

On the other hand, the Early to Middle Paleozoic conodont orders (e.g., Belodellida, Protopanderodontida, and Prioniodontida) include many species and genera with multimembrate apparatuses composed of coniform elements (Sweet, 1988; Dzik, 1989, 1991, etc.).

Among the species and genera in these orders, Ordovician *Strachanognathus parvus* enacted by Rhodes (1955) is closely similar to *Neostrachanognathus tahoensis* proposed herein, being composed of nongeniculate coniform elements with a distinct anterobasal denticle. *Strachanognathus parvus* was identified as a unimembrate apparatus by Bergström (1981). Dzik (1989) distinguished, however, six types of coniform elements with an anterobasal denticle in the *S. parvus* apparatus.

The S elements of *Dapsilodus* and *Walliserodus* of the Belodellida are similar to the elements of *Aduncodina unicosta* in shape of the base and cusp, although they have no anterobasal denticles. The Belodellida became extinct by the end of the Devonian.

The Icriodontidae of the Prioniodontida is one of the youngest families including coniform elements in the M and S positions of the apparatuses. The coniform elements in the S positions of *Pelekysgnathus* of the Icriodontidae somewhat resemble *N. tahoensis*, although they do not possess any anterobasal denticles. The family is regarded to disappear by the end of the Devonian.

The coniform elements from the Carboniferous are quite rare. Among less than five coniform type species described (Cooper, 1939, etc.), Pennsylvanian *Neoprioniodus? expandofundus* Webster reported by Rabe (1977) from the Eastern Andes of Colombia is somewhat similar to the Sa element of *N. tahoensis*. I am unaware of any reports of Permian or Early Triassic Induan coniform conodonts.

It is quite interesting that more than five coniform multielement species including *A. unicosta* and *N. tahoensis* appeared in the Spathian 120 to 50 million years after the extinction of Devonian or Carboniferous coniform conodonts. I consider that the Triassic coniform types evolved from the ramiform types and the morphologic similarity (homeomorphy) between the Triassic coniform types and the Early to Middle Paleozoic ones may be a result of adaptive convergence of the elements as the feeding apparatuses. It is difficult to show in detail the differences in function between coniform and ramiform types and those among coniform elements in an apparatus. It is thought, however, that conodont animals were predators and coniform and ramiform types functioned in grasping and/or cutting food (Jeppsson, 1979; Dzik, 1991; Purnell, 1995).

A probable evolution from ramiform to coniform elements in the Early Triassic may represent the divergence of feeding mechanisms in the conodont apparatuses. The Triassic

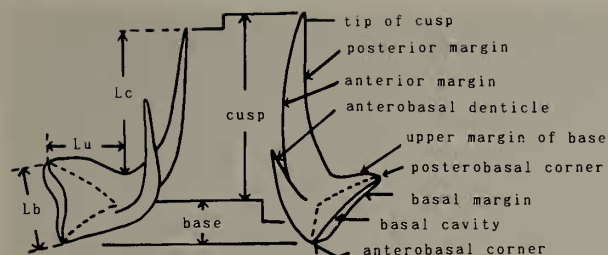


Figure 7. The morphology of the Sc elements of *Aduncodina unicosta* Ding (left) and *Neostrachanognathus tahoensis* gen. et sp. nov. (right). Lc: length of cusp, Lu: length of upper margin of base, Lb: length of basal margin

coniform elements probably evolved from the lineage of the Gondolellidae or Ellisonidae, which survived the Permian and diversified in the Early Triassic. Much more paleontological information on the Early Triassic conodont apparatuses is necessary to discuss this problem in more detail.

Systematic paleontology

Genus *Aduncodina* Ding, 1983

Type species.—*Aduncodina unicosta* Ding, 1983

Diagnosis.—*Aduncodina* a quadrimembrate apparatus composed of an adenticulated and three denticulated non-geniculate coniform elements. Base of coniform unit relatively large and long. Basal cavity moderately deep. Cusp suberect. Denticles of denticulated elements situated at the anterobasal portion and relatively long, proclined or curved inwardly (Figures 7, 8). Quadrimembrate elements are of the M, Sa, Sb, and Sc positions. M element bilaterally subsymmetric and adenticulated. Sa element bilaterally subsymmetric and denticulated with a proclined denticle. Sb element characterized by a conspicuous outward basal expansion and one to three hook-like anterobasal denticles curved inwardly. Sc element has lenticular basal margin and carries one to four hook-like anterobasal denticles curved inwardly.

Aduncodina unicosta Ding, 1983

Figure 8

Sa element

Cornudina anterodentata Ding, 1983. p. 41, pl. 6, figs. 18 (?)–19, 23–24.

Sb element

Aduncodina unicosta Ding, 1983. p. 41, pl. 6, figs. 10–14, 20 (?)–21.

Sc element

Cornudina cf. *oezdemirae* (Gedik), Ding, 1983. p. 42, pl. 7, figs. 25–26.

Cornudina angularis Wang and Cao, 1993. p. 249, pl. 60, figs. 2, 15.

Description.— M, Sa, Sb, and Sc elements have common morphologic characteristics such as small unit, thin wall, relatively large and long base, suberect slender cusp with

subcircular cross section, and moderately deep basal cavity.

M element bilaterally subsymmetric adenticulated coniform. Base lenticular in cross section (Figure 3). Basal margin very weakly convex toward anterior and 180 to 240 μm in diameter. Upper margin of base 140 to 180 μm in length. Cusp attains 230 to 400 μm in length.

Sa element bilaterally subsymmetric denticulated coniform. Base lenticular in cross section. Basal margin weakly convex toward anterior and 110 to 210 μm in diameter. Upper margin of base 100 to 180 μm in length. Cusp attains 150 to 300 μm in length. Anterobasal margin carries one proclined denticle, about one third to one half of length of cusp, and subcircular in cross section. Apex of basal cavity extends near junction of cusp and anterobasal denticle.

Sb element bilaterally asymmetric denticulated coniform. Base conspicuously expands outwardly and triangular in cross section. Basal margin weakly to strongly convex anteriorly and 130 to 200 μm in diameter. Upper margin of base 100 to 200 μm in length. Cusp attains 130 to 300 μm in length. Anterobasal margin carries one to three hook-like denticles, which are discrete, subequal in size and about one fifth of length of cusp, and extended inwardly and curved upwardly. Apex of basal cavity situated near junction of cusp and anteriormost denticle.

Sc element bilaterally asymmetric denticulated coniform. Base lenticular in cross section. Basal margin weakly to strongly convex anteriorly and 110 to 180 μm in diameter. Upper margin of base 110 to 200 μm in length. Cusp attains 140 to 280 μm . Anterobasal margin bears one to four hook-like denticles, which exhibit the same features as those of Sb element. Basal cavity also shows the same characteristics as that of Sb element.

Remarks.—The form species *Cornudina anterodentata* proposed by Ding (1983) is bilaterally subsymmetric non-geniculate coniform with one or two proclined denticles on the anterobasal margin. The morphologic characteristics of the form species well accord with those of the Sa element of the *A. unicosta* apparatus. The Sa element from the Tahoe Formation, however, does not have two anterobasal denticles but only one denticle as far as observed.

The form species *Cornudina angularis* proposed by Wang and Cao (1993) and *Cornudina* cf. *oezdemirae* (Gedik) described by Ding (1983) are identical with the Sc element of *A. unicosta* in having lenticular cross section of the basal margin and carrying one inwardly flexing anterobasal denticle.

The Sa, Sb, and Sc elements of the *A. unicosta* and *N. tahoensis* apparatuses are common in arrangement of the anterobasal denticles, respectively. They are different, however, in outline of the unit, relative size of the base, shape of the basal cavity, cross section of the basal margin, and shape of the cusp and anterobasal denticles.

Repository.—YNUC15832–15857.

Genus *Neostrachanognathus* gen. nov.

Type species.—*Neostrachanognathus tahoensis* sp. nov.

Diagnosis.—Diagnosis of *Neostrachanognathus* newly

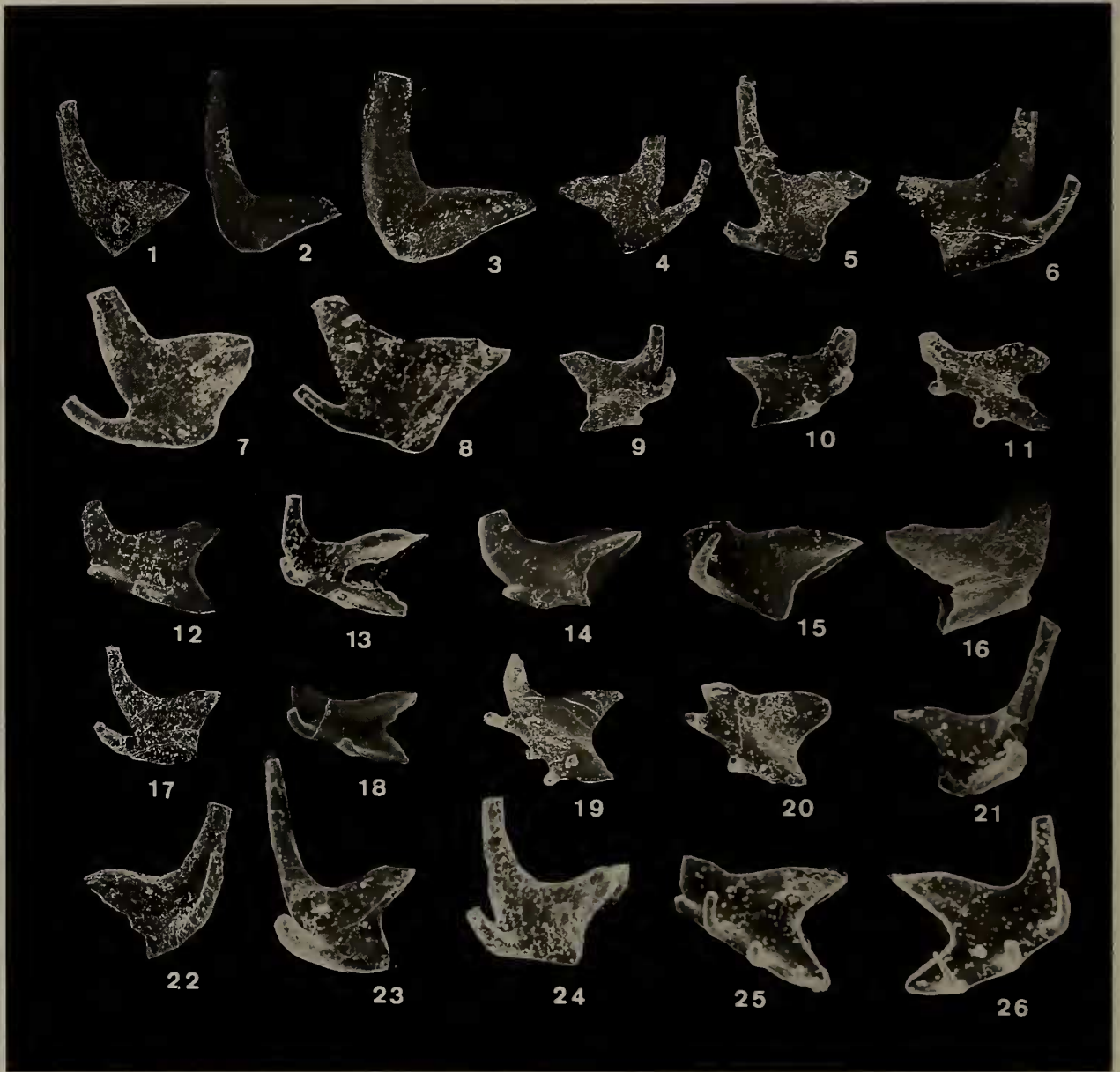


Figure 8. Elements of *Aduncodina unicosta* Ding from the Taho Formation, all $\times 100$. 1-3. M elements, YNUC15832-15834 from Loc. 1415. 4-8. Sa elements, 4: YNUC 15835 from Loc. 1415, 5: YNUC 15836 from Loc. 1119-1, 6: YNUC 15837 from Loc. 1415, 7-8: YNUC15838-15839 from Loc. 1185. 9-16. Sb elements, 9: outer lateral view, YNUC15840 from Loc. 1415, 10-12: inner lateral views, YNUC15841-15843 from Loc. 1415, 13: outer lateral view, YNUC15844 from Loc. 1186, 14-15: inner lateral views, YNUC15845-15846 from Loc. 1415, 16: outer lateral view, YNUC15847. 17-26. Inner lateral views of Sc elements, 17-20: YNUC15848-15851 from Loc. 1415, 21-24: YNUC15852-15855 from Loc. 1119-1, 25-26: YNUC15856-15857 from Loc. 1185.

proposed is based on *N. tahoensis* sp. nov. *Neostrachanognathus* is characterized by a quadrimembrate apparatus composed of an adenticulated and three denticulated nongeniculate coniform elements. Base of elements relatively small and short and the basal cavity shallow. Cusp proclined and tapered. Denticles of denticulated elements situated at anterobasal portion (Figures 7, 9). Coniform

elements referable to M, Sa, Sb, and Sc. M element bilaterally subsymmetric adenticulated coniform. Sa element bilaterally subsymmetric denticulated coniform and carries one small proclined anterobasal denticle. Sb element has inwardly bending one or two small to large anterobasal denticles. Sc element possesses long upper basal margin and carries inwardly flexing one or two small to large



Figure 9. Elements of *Neostrachanognathus tahoensis* gen. et sp. nov., all $\times 100$. 1-4. M elements, YNUC15858-15861 from Loc 1120. 5-9. Sa elements, 5-8: YNUC15862-15865 from Loc. 1120, 9: YNUC15866 from Loc. 1185. 10-15. Inner lateral views of Sb elements, YNUC15867-15872 from Loc. 1120. 16-23. Inner lateral views of Sc elements, 16-17: YNUC15873-15874 from Loc. 1185, 18: YNUC15875 from Loc. 1120, 19: holotype, YNUC15876 from Loc. 1120, 20-23: YNUC15877-15880 from Loc. 1120.

anterobasal denticles. One posterior denticle may be present on the base.

Neostrachanognathus tahoensis sp. nov.

Figure 9

Sb element

Cratognathodus sp. Buryi, 1989, pl. 2, fig. 6.

Holotype.—Sc element YNUC 15876; Figure 9-19; Taho Limestone, Tahokamigumi, Shirokawa-cho, Ehime Prefecture.

Description.—Four elements of this apparatus exhibit common characteristics such as thick wall, relatively small and short base, and proclined and tapered cusp.

M element bilaterally subsymmetric adenticulated coniform. Lower view of basal margin lenticular shape with broadly or narrowly rounded posterobasal corner and bluntly pointed anterobasal corner. Basal margin 150 to 230 μm in diameter and upper margin of base 50 to 100 μm in length. Cusp stout, ellipsoidal in cross section, and 250 to 300 μm in length.

Sa element bilaterally subsymmetric denticulated coniform. Basal margin lenticular in shape, rounded and bluntly pointed at posterobasal and anterobasal corners, respectively in cross section, and 150 to 200 μm in diameter. Upper margin of base 30 to 80 μm in length. Cusp attains 240 to 300 μm in length. Anterobasal margin carries one short proclined denticle, which ranges from 20 to 50 μm in length and is ellipsoidal to subcircular in cross section.

Sb element bilaterally asymmetric denticulated coniform. Lower view of basal margin lenticular in shape with broadly rounded or bluntly pointed posterobasal corner and bluntly or sharply pointed anterobasal corner. Basal margin 180 to 230 μm in diameter and upper margin of base 40 to 80 μm in length. Cusp 250 to 350 μm in length. Anterobasal margin possesses inwardly bending one or two denticles. Longer denticle 50 to 150 μm in length.

Sc element bilaterally asymmetric denticulated coniform. Basal outer surface expanded and basal margin shows laterally compressed triangular shape in cross section. Basal margin 180 to 340 μm in length. Upper margin of base long and 80 to 140 μm in length. Cusp proclined to suberect and 270 to 500 μm in length. Anterobasal margin carries one or two inwardly flexing denticles. Longer denticle 80 to 250 μm in length.

Remarks.—The form species *Cornudina oezdemirae* proposed by Gedik (1975) was based on 16 specimens from the lower Anisian of the Kocaeli Peninsula, Turkey and its morphologic characteristics correspond to the subsymmetric Sa element of *N. tahoensis*. The holotype of *C. oezdemirae* illustrated by Gedik (Pl. 7, Fig. 24), however, lacks the anterobasal part. In that case, it is difficult to compare the specimen with *N. tahoensis* because incomplete specimens of *Cornudina igoi* lacking anterior denticles are also quite similar to *N. tahoensis*. There is a possibility that *N. tahoensis* or *C. igoi* is a synonym of *C. oezdemirae*. The information about *C. oezdemirae* by Gedik (1975), however, is insufficient to clearly distinguish it from these Japanese species.

The Sa element of *N. tahoensis* with a relatively large denticle is quite similar to *C. igoi* carrying only one anterior denticle, and *N. tahoensis* occurs together with *C. igoi*. Hence, there is a probability that *C. igoi* represents the Pa element of the *N. tahoensis* apparatus. The occurrence of *C. igoi*, however, is very common compared with that of *N. tahoensis*. For example, the frequency of the M, Sa, Sb, and Sc elements in *N. tahoensis* is 9, 29, 28, and 67, respectively but the specimens referable to *C. igoi* attain 318 in the

sample from the locality number 1120 in which both *N. tahoensis* and *C. igoi* occur abundantly. Thus, *Cornudina igoi* occurs more than ten times more commonly than the Sa and Sb elements of *N. tahoensis*, although robustness of the elements is almost the same. I regard here that *C. igoi* should not be considered the Pa element of *N. tahoensis*.

Buryi (1989) illustrated one specimen of the form species *Cratognathodus* sp. but did not offer any description. It is probably referable to the Sb element of the *N. tahoensis* apparatus, judging from the arrangement of the anterobasal denticles.

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References cited

- Bergström, S.M., 1981: Family Strachanognathidae Bergström, 1981. In, Robinson, R.A. ed., *Treatise on invertebrate paleontology. Pt. W, Supplement 2, Conodonta*, p. W147. Geological Society of America and the University of Kansas Press.
- Buryi, G.I., 1989: *Triassic conodonts and stratigraphy of Shikhote-Alin*. 136 p. Academy of Sciences of the USSR, Far Eastern Branch. (in Russian)
- Cooper, C.L., 1939: Conodonts from a Bushberg-Hannibal horizon in Oklahoma. *Journal of Paleontology*, vol. 13, no. 4, p. 379-422.
- Ding, M., 1983: Lower Triassic conodonts from the Mountain Majiashan in Anhui province and their stratigraphic significance. *Earth Science-Journal of Wuhan College of Geology*, no. 2, p. 37-48. (in Chinese)
- Dzik, J., 1989: Conodont evolution in high latitudes of the Ordovician. In, Ziegler, W. ed., *1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V) Contributions III, Courier Forschungs-institut Senckenberg*, vol. 117, p. 1-28.
- Dzik, J., 1991: Evolution of oral apparatuses in the conodont chordates. *Acta Palaeontologica Polonica*, vol. 36, no. 3, p. 265-323.
- Dzik, J. and Drygant, D.M., 1986: The apparatus of panderodontid conodonts. *Lethaia*, vol. 19, p. 133-141.
- Gedik, I., 1975: Die Conodonten der Trias auf der Kocaeli-Halbinsel (Turkei). *Palaeontographica, Abt. A*, vol. 150, p. 99-160.
- Hatleberg, E.W. and Clark, D.L., 1984: Lower Triassic conodonts and biofacies interpretations: Nepal and Svalbard. *Geologica et Palaeontologica*, vol. 18, p. 101-125.
- Jeppsson, L., 1979: Conodont element function. *Lethaia*, vol. 12, p. 153-171.
- Koike, T., 1994: Skeletal apparatus and its evolutionary trends in a Triassic conodont *Ellisonia dinodoides* (Tatge) from the Taho Limestone, Southwest Japan.

- Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 173, p. 366-383.
- Koike, T., 1996 : Skeletal apparatuses of Triassic conodonts of *Cornudina*. In, Noda, H. and Sashida, K. eds., *Prof. Hisayoshi Igo commemorative volume on geology and paleontology of Japan and Southeast Asia*, p. 113-120.
- Kozur, H. and Mock, R., 1991 : New middle Carnian and Rhaetian conodonts from Hungary and the Alps. Stratigraphic importance and tectonic implications for the Buda Mountains and adjacent areas. *Jahrbuch der Geologischen Bundesanstalt*, vol. 134, no. 2, p. 271-297.
- Kozur, H. and Mostler, H., 1972 : Die Conodonten der Trias und ihr stratigraphischer Wert. I: Die Zahnreihen-Conodonten der Mittel- und Obertrias. *Abhandlungen der Geologischen Bundesanstalt*, vol. 28, no. 1, p. 1-53.
- Purnell, M.K., 1995 : Microwear on conodont elements and macrophagy in the first vertebrates. *Nature*, vol. 374, no. 27, p. 798-800.
- Purnell, M.K. and Donoghue, P.C.J., 1998 : Skeletal architecture, homologies and taphonomy of ozarkodinid conodonts. *Palaeontology*, vol. 41, pt. 1, p. 57-102.
- Rabe, E.H., 1977 : Zur Stratigraphie des ostandinen Raumes von Kolumbien. *Giessener Geologische Schriften*, no. 11, 223 p, Lenz-Verlag-Giessen.
- Rhodes, F.H.T., 1955 : The conodont fauna of the Keisley Limestone. *Quarterly Journal of the Geological Society of London*, vol. 111, p. 117-142.
- Sweet, W.C., 1981 : Family Xaniognathidae Sweet, 1981. In, Rhobinson, R.A. ed., *Treatise on invertebrate paleontology. Pt. W, Supplement 2, Conodonta*, p. W154-W157. The Geological Society of America, and the University of Kansas Press.
- Sweet, W.C., 1988 : The Conodonta. Morphology, taxonomy, paleontology, and evolutionary history of a long-extinct animal phylum. *Oxford Monographs on Geology and Geophysics*, no. 10, 212 p.
- Von Bitter, P.H., and Merrill, G.K., 1988 : Apparatus composition and structure of the Pennsylvanian conodont genus *Gondolella* based on assemblages from the Desmoinesian of northwestern Illinois, U.S.A. *Journal of Paleontology*, vol. 72, no. 1, p. 112-132.
- Wang, Z.H. and Cao, Y., 1993 : Triassic conodonts. In, Wang C.Y. ed., *Conodonts of Lower Yangtze Valley. Indexes to Biostratigraphy and Organic Metamorphic Maturity*. p. 249-267, Science Press, Beijing. (in Chinese with English summary)